PREDICTING DEVELOPMENT RATE OF COPEPOD EGGS [1]

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This paper is part of a continuing study of intrinsic controls of growth, development and, implicitly, productivity of marine zooplankton. Copepods are particularly suitable for comparative studies of embryonic development rate because most species hatch at a morphologically equivalent first naupliar stage. The effect of temperature on size varies markedly among different geographical populations of the copepod *Pseudocalanus minutus* Krøyer, and it was assumed that embryonic development rate would vary likewise (McLaren, 1965a). However, after trips in the spring of 1965 to Woods Hole, Mass., Halifax, N. S., and Millport, Scotland, it was clear that embryonic development rate varied only slightly, and attention was directed to other species. A summer trip to Frobisher, N. W. T., was made particularly to secure data on a large-egged form of *Pseudocalanus* living in Ogac Lake, a warm, landlocked fiord off Frobisher Bay (McLaren, 1965a). Successful experiments at Frobisher on the large *Calanus glacialis* Jaschnov (see Grainger, 1961) were doubly useful because of published data on *C. finmarchicus* (Gunnerus) from Scotland and Norway (Marshall and Orr, 1953). A brief return to Halifax in April, 1966, added two more species, *Acartia clausi* Giesbrecht and *Tortanus discaudatus* (Thompson and Scott).

Although the number of forms studied is rather small, the results are published at this time because they seem to have some general and theoretical interest. More work will be done to confirm the results and hopefully to extend their predictive value to other developmental stages.

Use will be made of Bělehrádek's (1935, 1957) equation, in which rate of a metabolic function (here, development time D in days) is given by

$$D = a(T - \alpha)^b$$

where a, b and α are constants and T is the temperature. The empirical superiority of this equation and the conceptual meaning of its parameters have been discussed by McLaren (1963, 1965b). Briefly, the formula is the simplest of several equations describing the three ways in which montonic responses to temperature may differ: a accounts for differences in mean slope, α for shifts on the temperature scale, and b depicts the degree of curvilinearity of the response quite adequately over the vital temperature range. This paper will show that the three parameters are related to separate biological properties as well. The equation is fitted by conversion to logarithms and successive approximation to that value of α having smallest sums of squares of deviations of observed from calculated development times.

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Materials and Methods

The methods used were simple but at times onerous. Animals were captured by fine-mesh nets and samples kept cool during the return to the laboratory. Individual females were removed from the samples within an hour or two of capture with the aid of dissecting microscopes and eyedroppers. The females were kept in small groups in bottles at temperatures about as cool as the waters from which they were captured. During earlier series of experiments on *P. minutus,* concentrations of diatoms from net samples were added to the bottles in the hope of stimulating egg-laying. It was later found that eggs would be produced without the addition of food, provided the females came from phytoplankton-rich water. The bottles were observed regularly and free eggs (most species) or females carrying egg sacs (*Pseudocalanus*) were removed by eyedroppers as they appeared. These were placed in small vials with about 10 cc. of filtered sea water. Only a small proportion of females produced eggs, usually within a day or so of capture. Pertinent collection and experimental data are given on Table I.

The vials were kept at controlled temperatures until the eggs hatched. Accurate constant-temperature baths were available at Woods Hole, Halifax, and Millport. Baths in less well-controlled ambient temperatures of cold rooms were also available, and somewhat variable temperatures of around 2–3° C. were obtained in domestic-type refrigerators. Only a domestic refrigerator was available at Frobisher, and higher temperatures were maintained there by periodic additions of ice or warm water to large, covered, styrene-foam containers kept in the cool out-of-doors. These portable containers were also useful in completing experiments begun at Ogac Lake and finished at the townsite at Frobisher, a day's boat-trip from Ogac Lake. A temperature of 0° was easily obtained in ice-water baths kept just under the freezing compartments of domestic refrigerators. Because of the long time required for development, most of the experiments at 0° and some of those at higher temperatures were carried out on eggs produced by females brought by air to Montreal in vacuum bottles. A few experiments begun elsewhere were finished in Montreal—the vials kept at the appropriate temperatures in vacuum bottles during air transport. Clearly it was impossible to maintain rigidly constant temperatures under some of the above experimental conditions. However, temperatures were kept within narrow limits and observed frequently (at least every 3–4 hours), 24 hours a day. Since the effect of temperature is virtually linear over a reasonably narrow range, the graphically estimated mean temperatures may be taken as extremely accurate measures of the effective temperatures during development.

Experimental salinities were not quite the same in all localities, but differed markedly only in a second series of experiments on *Pseudocalanus* from Ogac Lake.

TABLE I

Mean development times of copepod eggs at different temperatures. Each experiment is a single egg sac (Pseudocalanus) or a batch of eggs produced more or less synchronously by one or more females (other spp.)

Species	Locality	Times of capture	Experimental salinity (‰)	No. of experiments	Mean experimental temperature (° C.)	Time of 50% hatch of viable eggs (days)	
						Mean ±95% f.l.	range
Pseudocalanus minutus	Woods Hole, Mass.	Jan. 27–Feb. 10, '65	31.8	7	0	10.89 ±0.20	10.54–11.14
			31.8	3	3.18	6.61	6.49–6.75
			31.8	9	4.60	5.91 ±0.09	4.43–4.70
			31.8	1	11.38	3.07	—
			31.8	3	13.13	2.78	2.69– 2.83
Pseudocalanus minutus	Halifax, N.S.	Mar. 19–29, '65	30.4	9	0	10.71 ±0.22	10.56–11.14
			30.4	11	2.73	6.92 ±0.09	6.71– 7.16
			30.4	4	5.35	5.05 ±0.27	4.90– 5.31
			30.4	11	9.27	3.48 ±0.04	3.38– 3.58
			30.4	14	12.01	2.90 ±0.05	2.75– 3.00
Pseudocalanus minutus	Millport, Scotland	May 17–31, '65	30.4	4	0	11.15 ±0.19	11.03–11.24
			30.4	2	2.65	7.50	7.42– 7.58
			30.4	1	3.14	7.15	—
			31.3	5	4.53	6.05 ±0.14	5.92– 6.19
			31.3	5	6.64	4.84 ±0.20	4.64– 4.94
			31.3	7	10.05	3.35 ±0.13	3.20– 3.49
			31.3	5	12.95	2.75 ±0.10	2.63– 2.79
			31.3	2	14.90	2.61	2.57– 2.65
Pseudocalanus minutus	Frobisher, N.W.T.	June 24–July 8, '65	32.3	7	0	10.44 ±0.19	10.18–10.71
			32.3	9	2.49	7.50 ±0.23	7.13– 8.00
			32.3	8	5.42	5.32 ±0.13	5.19– 5.67
			32.3	5	7.90	4.14 ±0.20	3.98– 4.40
Pseudocalanus minutus	Ogac Lake, N.W.T.	July 18 & Aug. 3, '65	32.3	1	0	11.22	—
			25.7	3	0	10.86	10.61–11.21
			25.7	3	2.62	7.43	7.33– 7.62
			32.3	2	3.30	6.94	6.87– 7.00
			25.7	3	5.34	5.55	5.46– 5.67
			32.3	1	7.10	4.35	—
Pseudocalanus, large form	Ogac Lake, N.W.T.	July 18 & Aug. 3, '65	32.3	2	0	17.91	17.08–18.75
			25.7	1	0	17.27	—
			32.3	1	2.67	12.23	—
			25.7	1	3.31	10.46	—
			25.7	3	5.19	9.06	8.92– 9.30
Calanus glacialis	Frobisher, N.W.T.	July 8 '65	32.3	1	0	6.35	—
			32.3	1	2.60	4.30	—
			32.3	1	5.23	3.23	—
			32.3	1	7.92	2.61	—
Acartia clausi	Halifax, N.S.	April 5 & 7, '66	30.5	1	0	15.33	—
			30.5	3	4.88	5.98	5.88– 6.05
			30.5	3	10.80	2.78	2.69– 2.87
Tortanus discaudatus	Halifax, N.S.	April 5 & 7, '66	30.5	1	0	19.71	—
			30.5	3	4.85	8.15	8.00– 8.25
			30.5	3	10.80	3.93	3.82– 3.98

Much mortality had occurred during the first series of experiments at higher salinities. Since Ogac Lake is somewhat brackish, it was thought that filtered lake water would be more suitable, but mortality was still quite high. The possibility that salinity had an effect on development rate of eggs from Ogac Lake will be considered.

Not all eggs hatched, but those that did produced nauplii within a period of a few hours at most in a given vial. After eggs began hatching, experimental vials were observed frequently so that time of 50% hatch of viable eggs could be deter-

mined accurately. Above certain critical temperatures, which varied with locality, no eggs hatched. At lower temperatures, some batches of eggs failed partly or completely to hatch, and this sometimes appeared to be associated with bacterial or protozoan infestation. No antibiotics were used, but the sea water in some vials was changed when it appeared dirty. Arbitrarily, all experiments in which fewer than half the eggs proved viable are excluded from the following analyses, in view of the possibility that high mortality is accompanied by pathological or "unphysiological" retardation of development among the survivors.

TABLE II

Parameters of Bělehrádek's temperature function fitted to development time of copepod embryos

Species	Locality	Mean egg diameter ($\mu \pm 95\%$ f.l.)	Relative optical density (ratio $\pm 95\%$ f.l.)	Three constants fitted			b taken as -1.68	
				a	α	b	a	α
Pseudocalanus minutus	Woods Hole	127.4±3.7	—	325	− 9.2	−1.53	552	−10.52
P. minutus	Halifax	121.6±1.8	1.04±0.10	159	− 6.3	−1.23	516	−10.20
p. minutus	Millport	123.6±1.8	—	425	− 9.4	−1.62	536	− 9.99
P. minutus	Frobisher	130.4±3.3	(taken as 1.00)	8433	−16.6	−2.39	572	−10.77
P. minutus	Ogac Lake	108.5±2.3	0.95±0.11	3296	−14.0	−2.16	543	−10.27
Pseudocalanus, large form	Ogac Lake	155.3±2.6	1.04±0.14	82	− 5.0	−0.95	908	−10.47
Calanus glacialis	Frobisher	178.6±2.5	0.39±0.03	44	− 6.1	−1.07	308	−11.23
C. finmarchicus	Tromsø	ca. 145	—	155	− 8.7	−1.57	231	− 9.72
C. finmarchicus	Millport	ca. 145	—	6	− 1.2	−0.65	204	− 9.43
Acartia clausi	Halifax	79.4±3.4	2.21±0.35	1679	− 8.9	−2.15	322	− 6.02
Tortanus discaudatus	Halifax	102.4±4.7	1.29±0.18	2307	− 9.4	−2.12	477	− 6.55

Eggs were measured with optical micrometers at × 40 or greater. Diameters given are of unpreserved eggs. Maximum and minimum diameters were averaged for near-spherical eggs, but the three appropriate diameters were taken of the flattened spheroid eggs of *T. discaudatus*.

A simple and perhaps rather crude method was used to determine optical density of formalin-preserved eggs, using a photomicrographic exposure meter (Photovolt Corp., New York, model 514-M). Eggs were placed on depression slides in clean formalin-sea water. Each egg was measured, then centered alone in the microscopic field at × 250, in low, unfiltered illumination from a 6-volt wet-battery. The light cell was then applied to the photographic ocular and the meter deflection caused by moving the egg in and out of the center of the field was noted. Since the eggs are rather uniformly granular, it is assumed that no defraction problems were involved and that the meter deflections were a valid measure of the optical extinction caused by the volume of matter in the egg. Deflections were of the range of 5–20 units per egg; calibration is not exact, but one unit is of the order of 10^{-5} foot candles.

Results

Effects of temperature

The experimental results are summarized on Table I. Clearly there are differences in temperature response among the various species. Development rate of *P. minutus* varies only slightly in different parts of its range. The differences are in some cases significant (compare, for example, the rate at 0° at Frobisher and Millport), but not nearly as great as expected from preliminary experiments on *relative* rate of development (McLaren, 1965a).

Bělehrádek's temperature functions have been fitted to all the data on Table I, and the resulting parameters are on Table II. For simplicity, mean development times were used, weighted by number of experiments at each temperature; the error in this procedure is probably small and unsystematic. Published data (Marshall and Orr, 1953) on development times of *C. finmarchicus* are also analyzed on Table II. The data were published as ranges in hours and were averaged for purposes of calculation.

Since the calculated values of α on Table II are generally well below the minimal experimental temperature (0°), the resolution of the function is very low, and the wide ranges of the three fitted parameters may be largely spurious. McLaren (1965b) suggested that the degree of curvilinearity of response to temperature (b) might be the same among related groups. The "real" value of b may be taken as the mean of estimates on Table II, each estimate weighted by the square root of number of determining experiments (excluding *C. finmarchicus* from Millport, for which number of experiments was not given). This mean may differ slightly from the true statistical mean, but the arguments that follow would not differ for any chosen value of b within the range on Table II, since α, log a, and b are all linearly related. The new values of a and α are listed on Table II, and the empirical adequacy of the resulting curves is clear on Figure 1. Only two points deviate much from the curves; these points, at 2.7° and 3.3° for the large form of *Pseudocalanus,* represent individual experiments, whereas almost all other points are means. Assuming that b is in fact constant greatly increases the resolution of the function, even with inaccurate or biased data.

Taking b as 1.68 for all localities and species reduces the great range in values of α and regularizes them in a more logical way. Differences within species from various localities are then found to be very slight (range of 0.8° in *P. minutus* and 0.3° in *C. finmarchicus*), but differences between species are more marked. The most strictly arctic species, *C. glacialis,* has the lowest value of α. Unlike the other species, *A. clausi* and *T. discaudatus* do not extend to cold, northern regions, and this seems to be reflected in their higher values of α. At temperatures of $-1°$, which may be expected during the spring in arctic waters, *A. clausi* and *T. discaudatus* would take about three and four weeks simply to hatch their eggs.

Different values of α for embryonic development among thermal races of frogs (McLaren, 1956b) are significantly correlated with latitude or altitude, and therefore with environmental temperature. The *C. finmarchicus* studied by Marshall and Orr (1953) were said by these authors to be living at 2–3° and 6°, respectively, at Tromsø and Millport. The appropriate temperatures experienced by females of *P. minutus* can only be approximated. Temperatures for Halifax,

Woods Hole, and Millport are available as daily surface temperatures recorded by institutions at these localities. These are averaged for the periods during which females were captured. Temperatures were not taken at Frobisher or Ogac Lake during 1965. The waters below a few meters at Frobisher in late June and early July may be assumed to be at the winter minimum of *ca.* — 1.7°. A published estimate (McLaren, 1965a, his Figure 2) of mean temperature in Ogac Lake ex-

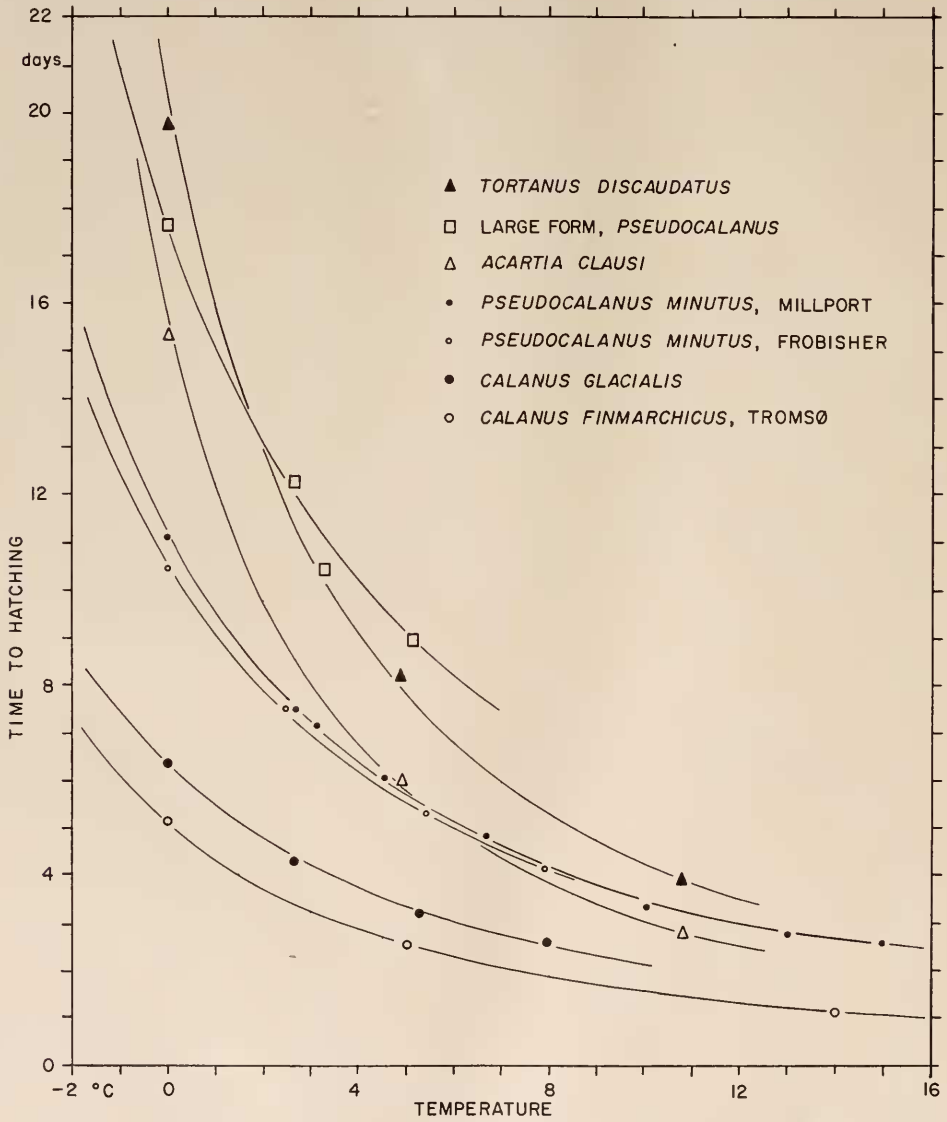

FIGURE 1. Bělehrádek's temperature functions fitted to development times of copepod embryos. The parameter b is taken as -1.68 for all curves, and the fitted values of α and a are given on Table II.

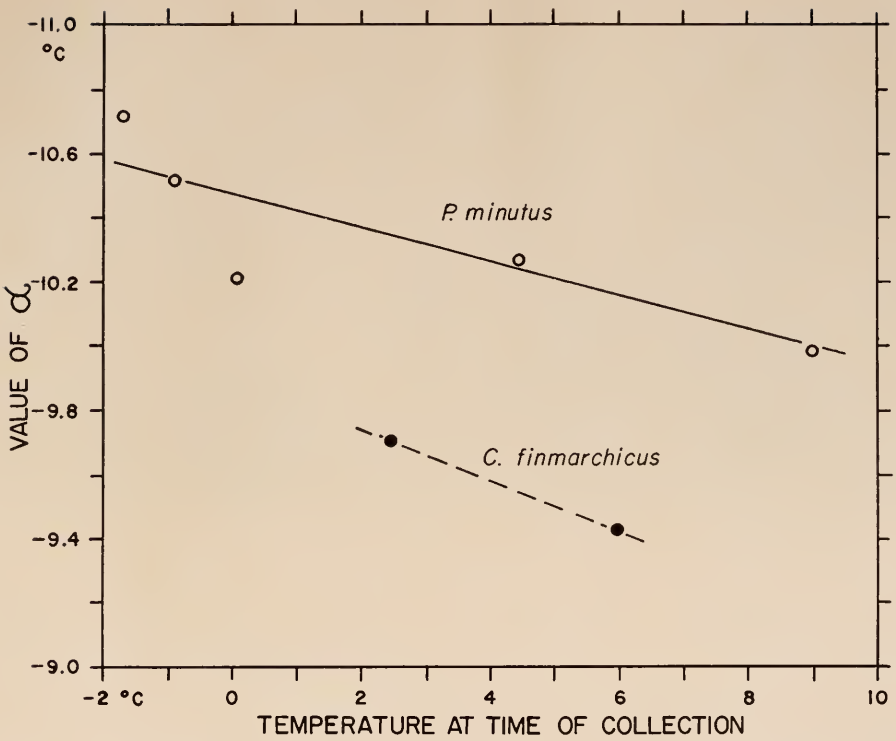

FIGURE 2. Relationship between the scale correction or "biological zero" α of Bělehrádek's function for development time of copepod embryos and estimated temperatures at the times egg-producing females were collected.

perienced by *P. minutus* maturing in early summer of 1957 may be used as a rough indication of temperatures at the same season in 1965. Values of α are plotted against these temperature estimates on Figure 2. The correlation for *P. minutus,* for which there are sufficient points to test, falls short of significant ($P \simeq 0.10$). But the relationship is, as expected, positive for both species. The amount of intraspecific "adaptation" is very small, and is of about the same order as that found among thermal races of frogs (McLaren, 1965b).

Effects of egg size

Berrill (1935) found that development time of ascidian eggs was linearly related to egg diameter, provided the eggs were comparable in yolkiness. McLaren (1965b) found that among thermal races of the frog *Rana pipiens,* α of Bělehrádek's function for embryonic development time was significantly correlated with egg diameter, at least within the United States. The same seems to be true among closely related forms of copepods (Fig. 3a). The correlation between a and egg diameter is significant ($0.05 > P > 0.01$) for *P. minutus,* excluding those from Ogac Lake. This is remarkable enough, considering the small number and re-

stricted range of values, and again seems to justify the assumption that b is the same for all populations.

In spite of their smaller size, the eggs of *P. minutus* from Ogac Lake developed at much the same rate as those from other areas. Differences in egg and body size of this species in the cold waters of Frobisher Bay and the warm waters of Ogac Lake are phenotypic (McLaren, 1965a). It may be that differences in egg size and its effects on a are not comparable to those occurring among the more widely

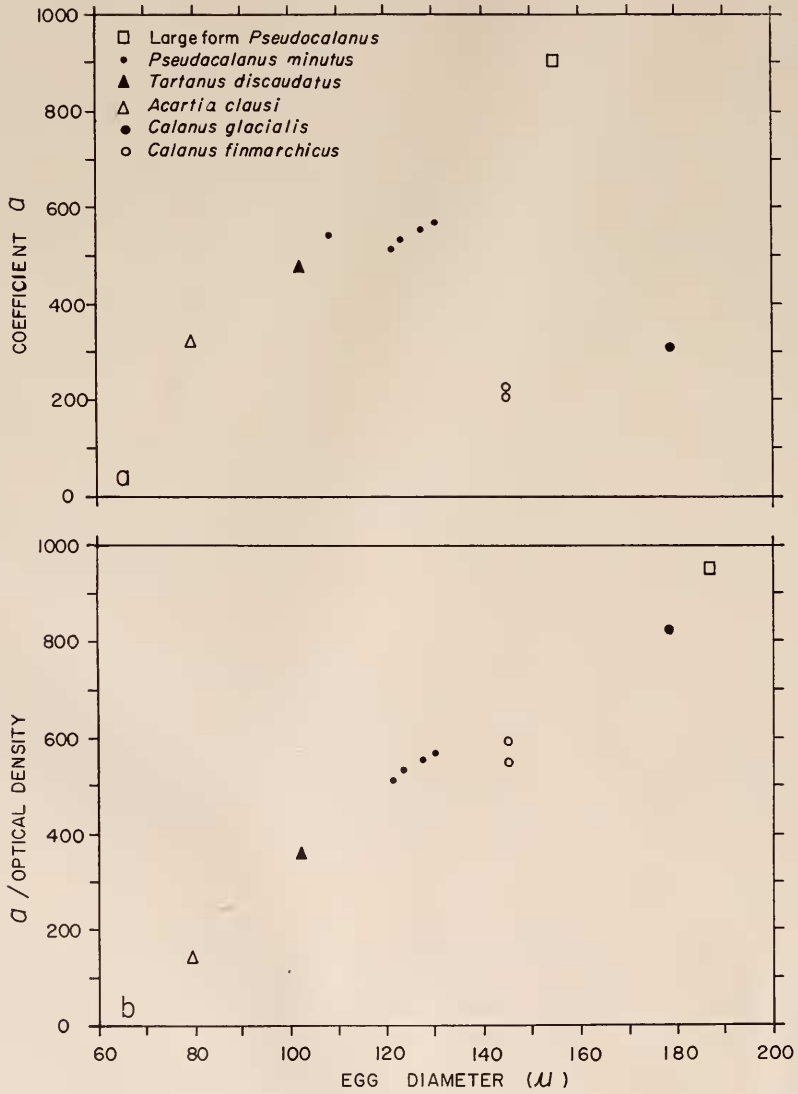

FIGURE 3. (a) Relationship between the proportionality coefficient a of Bělehrádek's temperature function for development time of copepod embryos and egg diameter. (b) The same after correction for yolk concentration (optical density). See text.

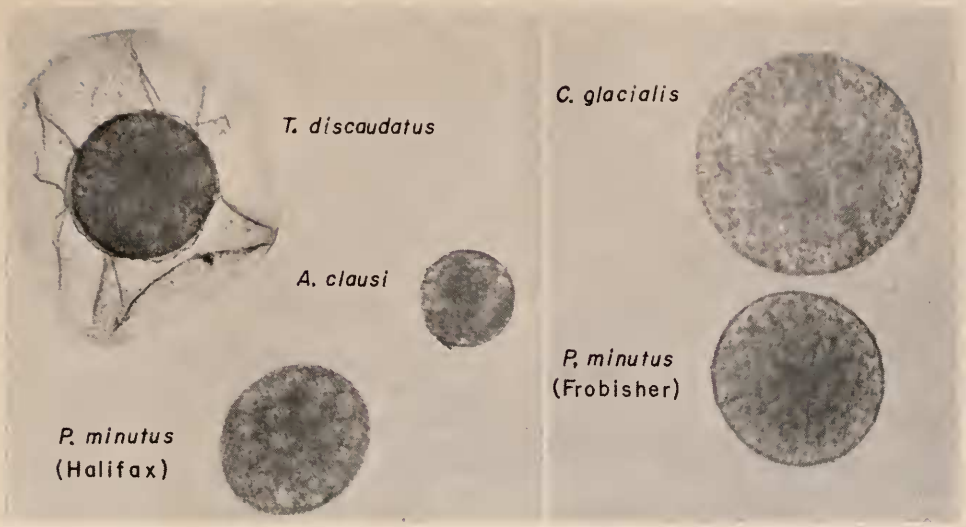

FIGURE 4. Representative copepod eggs to show differing optical density and size.

separated populations of the species. It is also possible that experimental salinities (see Materials and Methods) had an effect. Development was slower at 32.3‰ (Table I), which is abnormally high for the brackish population of Ogac Lake. There is evidence (Kinne, 1964) that growth rates, development rates, and sizes have optimal salinities. Whatever the explanation of the results from Ogac Lake, it seems possible to conclude that *P. minutus* and the large form of *Pseudocalanus* would have produced considerably larger eggs which would have developed only slightly more slowly than indicated, if they had been captured from the colder, more saline waters of Frobisher Bay.

The parameter a is not proportional to egg diameter. Assuming linearity, $a = 0$ at an egg size of about 35 μ for marine *P. minutus*. For the large form of *Pseudocalanus* and *P. minutus* from Ogac Lake, the intercept is at about 54 μ, and for *C. finmarchicus* and *glacialis*, at about 64 μ. Since it is impossible that real eggs of these intercept sizes would develop infinitely rapidly, the assumed linear relationships are probably roughly tangential to shallow, concave functions, with origins at 0 μ.

It is clear from Figure 3a that development times within species or among closely related forms may be partly predicted from egg size, but the same rule does not apply between distantly related species. For example, the eggs of *Calanus*, although much larger than those of *Pseudocalanus*, develop much more rapidly.

Effects of yolk concentration

Berrill (1935) concluded that development rate of ascidian eggs was retarded in proportion to the ratio of yolk to cytoplasm, although he made no quantitative measurements of yolk. All the copepod eggs studied here seem to be unpigmented, and are white to pale yellow in reflected light. Under transmitted light they differ

markedly in transparency (Fig. 4). It seems probable that transparency is related to concentration of yolk substances.

Newly produced eggs may be somewhat darker, and advanced embryos are more transparent, except for dark centers, which appear to be fat globules. Intermediate stages do not appear to vary systematically, and embryos ranging from few-celled to probable gastrula stages were chosen at random for measurements. Eggs of *Pseudocalanus, Calanus,* and *A. clausi* presented no special difficulties, although only a total of 11 eggs of the last species were available. Eggs of *T. discaudatus* are surrounded by a thick membrane, which is not completely transparent, and which often had a faint, reddish tinge. Thus, some of the extinction of transmitted light by these eggs is caused by the membrane. Fortunately, the complete membranes (Fig. 4) are cast by the hatching nauplii. A number were preserved for light measurements, and the results subtracted from measurements of intact eggs. Unfortunately, no corrections can be made for correlations of transparency of membranes and intact eggs.

The results are listed on Table II as mean extinctions per unit volumes of eggs, relative to the values for *P. minutus* from Frobisher Bay. Although they represent a 3-fold range in egg volumes, the eggs of the various populations and forms of *P. minutus* do not differ in optical density. This suggests that yolk concentration is the same among closely related forms, which also seems to be true of ascidians (Berrill, 1935). It also indicates the validity of the optical methods. In spite of large fiducial limits, due to small samples in most cases, there are marked and significant differences between species.

The exact relationship between yolk concentration and optical density cannot be proportional, but it may be nearly so, since cytoplasm is very transparent. The effect of yolk concentration on development time may be proportionate, but the effect of egg size is not (see above). Therefore the best way to express the possible effect of yolk is by dividing development time at a given temperature (or a among forms which differ in temperature characteristics) by yolk concentration (relative optical density). The results on Figure 3b clearly represent a marked regularization of the data on Figure 3a. Figure 3b also assumes, from arguments given above, that *P. minutus* is equivalent in size and development rate to the species in nearby Frobisher Bay, and that the large form of *Pseudocalanus* would be proportionately larger and slower in development if it occurred in Frobisher Bay.

The relationship on Figure 3b seems adequately described by

$$a = Y\ (6.51\ D - 317)$$

where a is the proportionality coefficient of Bělehrádek's function in days, Y is the optical density relative to eggs of *Pseudocalanus,* and D is egg diameter in μ. Again, the real effect of D is probably not linear, and the relationship may take its origin from $0\ \mu$.

Discussion

Bělehrádek's temperature function clarifies analysis of the data. From the results, it should be possible to predict development rate of eggs of other species of copepods with a minimum of experimental data. Of perhaps more general interest is the further support for the conclusion of McLaren (1965b) that the

three conceptually separable parameters of Bělehrádek's function have separable biological meaning.

Temperature adaptation *per se* can be considered in relation to a single parameter, the scale correction α. This seems much simpler than discussion of "Q_{10} shifts," "translation," "rotation," and like terms, some of which are artifacts of the semilogarithmic plot and combine differences in slope (a), curvilinearity (b), and position on the Celsius scale (α).

Among closely related forms differences in a may be predicted from size alone. The large form of *Pseudocalanus,* with eggs and bodies about three times the volume of those of co-existing *P. minutus,* has the same chromosome number, but the chromosomes are much larger and contain several times as much DNA (McLaren, Woods, and Shea, 1966). A similar mechanism may account for the larger size of *C. glacialis,* which has the same chromosome number but larger eggs than *C. finmarchicus.* The inherent differences in size and development rate are perhaps related to DNA content in the manner suggested by Commoner (1964). However, a is not proportional to volume or DNA content, so that another form of control must be superimposed.

It is of interest to note that Berrill (1935) found a similar pattern of development among ascidian eggs. Among eggs larger than about 250 μ, development time was linearly related to egg diameter, with an intercept at about 125 μ. For smaller eggs between 100 and 170 μ the relationship was slightly curvilinear, with an apparent intercept at about 60 μ. This is comparable with copepod egg development, with an apparent intercept at about 50 μ (Fig. 3b). Berrill argued from proportionality (although this is not strictly true) of development time and egg diameter that control is imposed by surface-to-volume restrictions on CO_2 exchange of the whole embryo, and offered some experimental evidence for this. Recently Daykin (1965) applied mass transfer theory to the uptake of oxygen by fish eggs. It is not possible to define conditions applying to ascidian and copepod eggs, but representative solutions of Daykin's equations imply that the mass transfer coefficient is itself a positive function of egg diameter, with a negative second derivative. If the same form of coefficient applies to the outward transfer of CO_2 (which is much more likely than O_2 to be limiting), then the control suggested by Berrill would not result in strict proportionality between development time and egg diameter. Instead development time would increase curvilinearly with diameter among small eggs and more nearly linearly among larger eggs, more or less in the manner suggested for ascidian and copepod eggs. This suggests that Berrill's general ideas are sound, and that detailed analysis and prediction might be possible.

The influence of yolk does not seem explicable in energetic or biochemical terms. Although more yolky eggs take longer to hatch, many analyses of fat, protein, and energy have shown that very little is used by most developing embryos before they hatch (*e.g.,* Hayes, 1949). There may well be qualitative differences in the yolk of the several kinds of copepods, but its effect seems proportional to its crudely defined concentration. This seems to support Berrill's conclusion that yolk simply "dilutes" the metabolically active cytoplasm of the egg and embryo.

Bělehrádek (1935, 1957) believed he had a theoretical basis for his temperature function in observations that diffusion and viscosity, but not chemical reaction rates *in vitro,* are affected in a comparable, double logarithmic way. McLaren (1965b)

suggested that yolk, by affecting diffusion characteristics, might be involved in temperature adaptations. There is no evidence that α of copepod eggs is affected by concentration of yolk; the relationship (Table II) is positive but far from significant. If Bělehrádek's general ideas are correct, it may be that qualitative differences of yolk are involved, or that control resides in biophysical properties of the cytoplasm, rather than yolk.

Summary

1. The development times to hatching of eggs of several kinds of copepods were studied at controlled temperatures. Data are analyzed from several geographical populations of *Pseudocalanus minutus,* a large form of *Pseudocalanus, Calanus finmarchicus, C. glacialis, Acartia clausi,* and *Tortanus discaudatus.*

2. Bělehrádek's temperature function, expressed as $D = a(T - \alpha)^b$, where D is development time, T the temperature, and α, a and b are constants, was fitted to the results. Assuming that b is the same (-1.68, the mean of fitted values) for all species results in several regularities.

3. The scale correction or "biological zero" α varies little within species, but seems positively related to environmental temperature. *C. glacialis,* with the most northerly range, has the lowest value of α, and *A. clausi* and *T. discaudatus,* which are the most southerly, have highest values of α. Temperature adaptation *per se* may be considered in relation to this parameter alone.

4. The proportionality coefficient a varies significantly with egg diameter within species or between closely related species. Differences in a and egg size are related to differences in DNA content between *P. minutus* and the large form of *Pseudocalanus,* and the same may be true between other closely related forms.

5. The coefficient a is not exactly proportional to egg diameter or DNA content, but the relationship resembles predictions from mass transfer theory, and supports Berrill's (1935) belief that control is superimposed by surface/volume restrictions on CO_2 exchange by the whole embryo.

6. Differences in optical density of eggs are attributed to yolk concentration. The parameter α is proportionate to relative optical density, which supports Berrill's (1935) conclusion that yolk simply "dilutes" metabolically active cytoplasm. Yolkiness does not appear to affect other parameters, which it might do if it imposed restrictions on diffusion, as implied by the possible biophysical basis of Bělehrádek's temperature function.

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